Agriochœrus guyotianus; A. trifrons, sp. nov.; A. ryderanus. Coloreodon macrocephalus.

North Fork of John Day River Epoch. Eucrotaphus trigonocephalus, sp. nov.; E major. Coloreodon ferox; C. macrocephalus.

Ticholeptus Beds. Merycochœrus montanus, sp. nov.; M. rusticus; M. proprius. Merychyus arenarum, sp. nov.; M. pariogonus, sp. nov.; M. zygomaticus. Cyclopidius simus; C. emydinus, sp. nov. Leptauchenia major; L. decora; L. nitida. Pithecistes brevifacies; P. heterodon; P. decedens, sp. nov.

Loup Fork Beds. ? Merychyus elegans; M. medius; ? M. major.*

The stratigraphic relations of these species may be represented under their generic heads in the following table:

	No. of species.	White River Epoch.	John Day Epoch.	? North Fork Epoch.	Ticholeptus Epoch.	Loup Fork Epoch.
Oreodontinæ.						
Oreodon Leidy........	3	———				
Eucrotaphus Leidy....	3	———	———	———		
Merycochœrus Leidy..	7		———	———	———	
Merychyus Leidy......	6				———	———
Leptauchenia Leidy...	3				———	
Cyclopidius Cope......	2				———	
Pithecistes Cope.......	3				———	
Agriochœrinæ.						
Agriochœrus Leidy....	6	———	———			
Coloreodon Cope......	2		———	———		
	35					

On the Structure of the Skull in the Elasmobranch genus Didymodus. By E. D. Cope.

(Read before the American Philosophical Society, March 7, 1884.)

The genus *Diplodus* was described by Agassiz from specimens of teeth from the European Coal Measures. In America, Newberry and Worthen† have described four species from the Carboniferous of Illinois and Ohio; and I have reported two species from the Permian beds of Illinois and Texas. Recently Mr. Samuel Garman has described a shark, said to have been taken in the Japanese seas, under the name of *Chlamydoselachus*

* The questions refer to the geological age.

† Geology of Illinois, vol. ii.

anguineus, whose teeth, as represented, do not differ generically from those of Diplodus. This is an interesting discovery, indicating that this genus, and not Ceratodus, is the oldest type of vertebrate now known in the living state.

My collections from the Permian beds of Texas include not only numerous teeth, but jaws and crania. Among these I recognize two types of teeth, which I cannot distinguish from those of the *D. compressus* Newb., and *D. gibbosus* Agass. Whether these species belong to the same genus, is a question, which I will discuss at the close of this article. I provisionally refer the *D. compressus* to a distinct genus, Didymodus, and will so call it in this article.

The determination of the characters of this genus is a point of much interest The teeth resemble those of the existing sharks more than do those of any other genus of the Palæozoic ages, but the antecedent improbability of the modern type having existed at such an early period of the earth's history, is shown to be well founded by the present investigation, which also throws much light on the question of the general phylogeny of the fishes.

I. Description.

Twelve more or less complete crania of species of Didymodus are in my collection, and one set of jaws with small teeth and part of the cranium attached. One of the crania, unfortunately much broken, exhibits also some large teeth. All were found by the late Jacob Boll in the Permian beds of Texas.

The skull of this species forms a continuum, which, however, displays distinct segments. First, however, as to the tissue of which it is composed. Both on the surface and in transverse fractures, it is more or less finely granular, the granules distinctly visible to the naked eye. These granules are composed of gypsum, as is also the matrix of a darker color in which they lie imbedded. Two hypotheses may be entertained regarding this structure. *First*, These granules may be regarded as the casts of coarse cartilage cells, and the matrix be in the place of the intercellular cartilage, replaced like the woody tissue in petrified wood. *Second*, The granules may be looked upon as replacements of osseous granules, such as cover the chondrocranium of most Elasmobranch fishes, while the matrix may be a replacement of the cartilage. The latter hypothesis is the more probable of the two, for two reasons: First, There is little probability of an unsupported chondrocranium retaining its form sufficiently long to permit the filling of its cells with a mineral deposit. Second, The granular type of ossification is well known in existing Elasmobranchs. It is only necessary to believe that the chondrocranium is penetrated by this kind of ossification. This state of things exists in the jaws also, which I describe later. This structure has already been observed by Kner in the genus Pleuracanthus.

The osseous cranium is abbreviated anteriorly, and elongated posteriorly, The orbit occupies part of the anterior third of the length. It is bounded in front by an obtuse preorbital process, and posteriorly by a laterally expanded and decurved postorbital process. The latter bears an articular facet on its posterior and inferior face. The top of the muzzle is excavated by a fontanelle which does not extend posterior to a line connecting the preorbital processes.

There is a prominent cup-shaped occipital condyle. On each side of the cranium a short distance anterior to it, is a prominent process extending outwards and a little backwards, which is excavated on its inferior side, but whose posterior side is decurved, so that the inferior concavity looks partially forwards. Into this cavity, and abutting against the decurved posterior edge, is a lateral process of the basal axial bone of the skull, which I take to be homologous with the lateral alæ which occupy the same position in the sharks. Anterior to this junction no doubt the hyomandibular bone was suspended, for I suspect that it was articulated to a small condyle which is wedged into the fissure between the inferior and superior elements described, a centimeter anterior to their posterior extremities. This condyle is a distinct element of a subglobular form.

The interorbital plane is continued posteriorly, bounded on each side by a depression which probably corresponds to the temporal fossa of higher vertebrates. The edges of this plane are thus well within the lateral borders of the cranium. The plane rises a little posteriorly, and is split into two narrow wedge-shaped processes, which project freely upwards and backwards. The rather short remaining part of the roof of the skull has a keel or sagittal crest on the middle line, which descends gradually to the foramen magnum.

The base of the skull forms a continuum from the edge of the large occipital cotylus to the acuminate anterior extremity. The lateral basal alæ are subcylindric, and are separated from the basicranial axis by a fissure for a short distance, and then unite with it. Two or three foramina anterior to this reunion, are in line with the defining fissure just mentioned. The basis cranii sends out a process on each side below the postorbital processes, giving a cross-shape to this part of the base of the skull. Anterior to this point it is free from other elements and contracts to an acuminate apex.

The cranium is segmented, but a clean specimen is necessary to permit the straight sutures to be seen. In the first place, there is a distinct occipital bone, which includes exoccipital and basioccipital elements combined. The latter includes the large occipital cotylus, as in the Rhachitomous batrachian Trimerorhachis, and differs from the structure seen in the Lepidosirenidæ, where exoccipital elements only are present. The occipital extends but a short distance on the inferior face of the axis. It is preceded directly, and without imbrication, by a continuous axial element. If we recognize in the granular character of the tissue evidence of true ossification of the chondrocranium, we have here true continuous sphenoid and presphenoid bones.

Returning to the superior face of the cranium, we observe that the exoccipital elements form a wedge-shaped body, divided on the middle line by suture, with the apex forwards. Traces of this division are figured by Gegenbaur as present in Heptanchus.* Anterior to this the middle of the cranial roof is apparently occupied by another triangular bone with the base posterior and the apex anterior, and concealed beneath the free extremity of the element in front of it. The lateral sutures only are distinguishable, appearing as grooves (fig. 2). This is the pariëtal bone. External to this and the occipital, and filling the space behind as well as anterior to the postero-lateral angle of the pariëtal, is the element which is produced outwards and backwards as already described. Were I describing a true fish, this bone might be intercalare (epiotic) or pterotic. Perhaps it is both combined, or it may be the cartilage bone called by Günther, in Ceratodus, the "tympanic lamina." † The element anterior to the pariëtal is the cartilaginous representative of the frontal, and the fact that it terminates posteriorly in two free processes is significant of the true homology of the bones which terminate in like manner in the crania of the Lepidosirenidæ.‡ In this family and in the Ceratodontidæ these bones are more or less separated on the middle line by the median posterior element. In Ceratodus the separation is wide; in Lepidosiren the interval is uninterrupted, but narrow in front. In Protopterus these elements are in contact on the middle line, but diverge posteriorly. Bischoff, Stannius§ and Günther identify these elements with the frontals in the genera they have described. Huxley‖ calls them supraorbitals, so that it becomes necessary to name the median posterior element a fronto-pariëtal, as a combination of two bones usually found distinct in fishes. The furcate structure of the frontal cartilage in Didymodus goes to show that the identification by Bischoff and Günther is the correct one. There are also in this genus distinct paired membrane bones which do not take part in the bifurcation in question, and which appear to represent the frontals of Ceratodus. Each of these is a flat, subcrescentic supraorbital plate, which has a concave superciliary border. It is separated by a considerable interval from its fellow of the opposite side. Its anterior extremity is notched by a fossa which I suppose to represent the anterior (posterior in position) nostril. The ? frontal of the right side is displaced, and appears as a lamina lying on the frontal cartilage, showing that it is a membrane bone. From its relation to the nostril the question arises, whether it be not the homologue of the nasal.

For hyomandibular bone, palatopterygoid arch, and mandibular arch, we have to rely principally on one specimen. On one of the skulls, two

* Ueber den Bau des Schedels der Selachier, 1872, Pl. I.

† Philosophical Transactions of the Royal Society, 1871, p. 511, indicated on the plates by the letter *d*.

‡ *Lepidosiren paradoxa* by Bischoff, Prof. in Heidelberg; Leipsic, 1840.

§ Handbuch der Anatomie der Wirbelthiere; Rostock; Erstes Buch, die Fische, 1854, p. 49.

‖ Anatomy of Vertebrated Animals, 1871, p. 145.

curved rib-like bones lie parallel and divergent posteriorly on the right side of the frontal, in the temporal fossa. I cannot identify them. They are not present on the opposite side. As already described, there is a facet on the infero-posterior face of the postfrontal process. This indicates the point of articulation of the palatopterygoid arch, as it exists in the group Opistharthri of the sharks as defined by Gill, and as is clearly proven by the specimen now to be described.

This includes the entire palatopterygoid and mandibular arches of one side, and the greater part of that of the opposite side, together with a considerable part of the right hyomandibular bone and probable extremity of the ceratohyal. The anterior parts of both jaws support numerous small teeth, which closely resemble those described by Agassiz as belonging to his *D. gibbosus*. They differ from those of the *D. compressus* in their smaller size. The palatine bones do not project much beyond the mandible, which, taken in connection with the form of the muzzle above described, renders it probable that the mouth was nearly terminal.

In the palatopterygoid arch there is no noticeable separation or suture between the palatine and pterygoid elements. The inferior border of the palatine is swollen below the orbit; its superior plate rises into a strong suborbital ala, which is concave externally, with thin superior edge. This edge rises posteriorly, giving the outline an elevated convexity, whose greatest upward prominence is above a point a little posterior to the middle of the jaw, and which probably articulated with the postorbital process of the cranium. Its surface gives indication of an articular surface appropriate to the corresponding one of the cranium. The superior border then descends rapidly to a vertical posterior border, which forms a somewhat prominent rim. This descends to the mandible, forming a regular ginglymus, the mandible bearing the cotylus. The mandible is rather robust; its inferior edge is rather thin, and becomes incurved anteriorly. Its superior border is regular, except that it rises a little at the coronoid region, and is impressed, corresponding with a concavity of the surface, and arch of the border of the pterygoid region, just anterior to the posterior prominent ridge which forms its posterior edge.

The hyomandibular bone is only exposed for its inferior half. It issues from behind the palatopterygoid as a narrow shaft with obliquely truncate extremity.

It is thus evident that the arrangement of the jaws is as in the two exceptional existing genera, Hexanchus and Heptanchus.

The external nostril already referred to, is a distinct, rather small fossa, on the lateral part of the superior face of the muzzle, near the extremity of the osseous portion. It is visible on both sides of the best-preserved specimen. It is continued forwards as a shallow groove. At the apex of the muzzle, is a fossa looking downwards, where roofed on each side by the ? nasal bones, which may represent the posterior nasal cavity. Or the latter may probably be represented by a lateral fossa just in front of the preorbital process. In either case it is evident that the nares are separated, and that the posterior one cannot be said to be within the oral cavity, as is the case in the known families of the Dipnoi. It is probable that there is a frontoparietal foramen at the posterior bifurcation of the frontal bones, corresponding to the conarium or pineal body of the brain. In a cranium broken across just anterior to the bifurcation, a canal passing forwards and downwards is exposed. There is a foramen, or possibly only a deep fossa on each side of the middle line on the occipito-sphenoid suture. The foramen magnum is rather small and opens upwards. Its border displays no articular surfaces. At the middle of a line connecting the posterior borders of the postorbital processes is a small shallow fossa, or probably foramen, from this there extends on each side backwards and outwards, a shallow groove apparently for a vessel, which terminates at the anterior one of three foramina already mentioned as in line with the fissure which distinguishes the lateral ala of the basicranial axis posteriorly. A similar groove connects the first and second of these foramina, and in one specimen the groove from the median foramen joins this connecting groove. In front of the median foramen is a rather larger one on the median line, situated at the fundus of a short longitudinal groove. It is placed just posterior to a line connecting the preorbital processes. The grooves easily become obsolete by weathering.

II. Affinities.

In determining the systematic position of this animal, it will be convenient to take a survey of the characters of the primary divisions of the fishes. In 1840 Bischoff published the first account of the osteology of Lepidosiren. In this description he called the frontal bones malars with a question, and the pariëtals frontopariëtals. He described the skull as having an os quadratum. In 1854, Stannius in the Handbuch der Zoötomie* correctly determined the frontals and pariëtals, and stated further that the "lower jaw and hyoid bone articulate directly with continuous processes of the chondrocranium." This appears to be the first correct description of the cranial structure of the Dipnoi. In 1864,† Huxley restated the view of Stannius as to the nature of the mandibular articulation; adopted the opinion of Bischoff that the frontal is a frontopariëtal, and took a new position in calling the frontals supraorbitals. He also restates in general, the description of the skull of the Holocephali already given by Stannius.

The system of Johannes Müller, adopted by Stannius, was a great improvement over preceding ones. It embraced, however, the error of including the Holocephali in the same sub-class (Elasmobranchi) with the sharks. This was adopted by Gill in 1861,‡ by Huxley in 1864§ and in 1871.‖ All of these authors adopt at these dates the sub-class Ganoidea.

* Erstes Buch, die Fische, p. 49.

† Elements of Comparative Anatomy, p. 210.

‡ Catalogue of the Fishes of the East Coast of North America, p. 24.

§ Elements of Comparative Anatomy.

‖ The Anatomy of Vertebrated Animals, p. 120.

In 1871* the writer gave the following as the primary divisions of the sub-class Pisces: Holocephali, Selachi, Dipnoi, Crossopterygia, Actinopteri. The Holocephali was raised to an equivalency with the other sub-classes on account of the absence of distinct hyomandibular bone. The Dipnoi were defined by the median pelvic element, by the distichous arrangement of the segments of the pectoral and ventral fins, when present, on a median axis, and by the supposed presence of a distinct hyomandibular bone. The latter definition must be abandoned, for though an ossification exists, it has been shown by Stannius, Huxley and Günther, to be merely a deposit in the continuous chondrocranium. The sub-class Crossopterygia was substituted for the sub-class Ganoidea of Agassiz and Müller, as the latter was believed to have no actual existence as a division of fishes. After comparing the osteology of Polypterus, Lepidosteus and Amia, I remark (p. 320) "It is thus evident that the sub-class Ganoidea cannot be maintained. It cannot be even regarded as an order, since I will show that Lepidosteus, Accipenser, and Amia, are all representatives of distinct orders. I hope, also, to make it evident that Polypterus should be elevated to the rank of a sub-class or division of equal rank with the rest of the fishes and with the Dipnoi, already adopted." The sub-class Ganoidea has not yet fallen into disuse, but there are strong symptoms that it will do so.† Among others I select the following extract from Huxley's paper on the ovaries of the smelt, published in 1883.‡

"As is well known, Lepidosteus presents an example of a Ganoid with oviducts like those of the higher Teleostei; in *Osmerus*, on the other hand, we have a Teleostean with oviducts like those of the ordinary Ganoidei. It is tolerably obvious, therefore, that the characters of the female reproductive organs can lend no support to any attempt to draw a sharp line of demarkation between the Ganoids and the Teleosteans.

"Boas has recently conclusively shown that the same is true of the supposed distinctive character afforded by the conus arteriosus; and it has long been admitted that the spiral valve which has been described in the intestine of *Chirocentrus* is the homologue of that which exists in all the Ganoids, though greatly reduced in *Lepidosteus*. Indeed I am inclined to believe that the circular valve which separates the colon from the rectum in the smelt is merely a last remainder of the spiral valve. Thus, among the supposed absolute distinctions between the Ganoids and the Teleostei, only the peculiarities of the brain, and especially the so-called chiasma of the optic nerves, remain for consideration. My lamented friend Mr. Balfour, in the last of his many valuable labors, proved conclusively that the brain of *Lepidosteus* is, both in structure and development, a Teleostean

*Proceedings Amer. Assoc. Adv. Science, p. 326. Transac. Amer. Philosoph. Soc., p. 449.

†The term ganoid can be used as an adjective to describe the scales already known by that name, and thus be preserved.

‡Proceedings Zoölogical Society of London, 1883, pp. 137, 138, 139.

brain. But it is singular that no one, so far as I know, has insisted upon the fact, not only that the Teleostean brain is essentially similar to that of the Ganoids, but that it is exactly in those respects in which the Ganoids and Teleostei agree in cerebral structure that they differ most markedly from the Plagiostomi and Chimæroidei.

"With respect to the chiasma of the optic nerves, the exact nature of that structure has not yet been properly elucidated either in the Selachians or in the Ganoids. But, whatever may come of such an investigation, the establishment of the existence of a true chiasma in the Ganoids, and of its absence in Teleosteans, can have but little bearing on the question of their affinities, since Wiedersheim has shown that a simple decussation of the fibres of the optic nerves, as in ordinary Teleosteans, takes place in many lizards."

In 1877* I proposed the following primary divisions of the fishes, and have seen no reason to alter my views as to their value as a correct expression of the affinities and diversities of this class of Vertebrata. The system differs only from that of 1871 in the consolidation of the Crossopterygia and Actinopteri into a single sub-class, the Hyopomata; and in a few corrections of the definitions given. They are as follows:

I. Suspensorium continuous with the cartilaginous cranium, with no hyomandibular. No rudimental opercular bone; no maxillary arch; pelvic bones present; axial series of fore limb shortened, the derivative radii sessile on the basal pieces; axial series of hinder limb prolonged in male.. *Holocephali.*

II. Suspensorium articulated with the cranium; no maxillary arch; no opercular nor pelvic bones; bones of limbs as in the last............ *Elasmobranchi.*

III. Suspensorium rudimental, continuous with cranium, supporting one or more opercular bones; cranium with superior membrane bones; no maxillary arch; a median pelvic element; the limbs supported by segmented unmodified axes.................................. *Dipnoi.*

IV. Hyomandibular and palatoquadrate bones articulated with cranium, supporting opercular bones; a maxillary arch; no pelvic element; axes of the limbs shortened, the derivative radii sessile on the basal pieces.. *Hyopomata.*

In the definition of the Dipnoi, it is necessary to make the correction in accordance with the best observations on fresh specimens, above referred to, as I have not been able to determine the question from dried specimens in the Hyrtl collection. The suspensorium cannot be properly said to be articulated to the cranium in the sense in which it is said to be such in the Elasmobranchi. In the latter it is articulated by ginglymus; in

*Proceedings of the American Philosophical Society, 1877, p. 25; and in the Annual Reports of the Commissioners of Fisheries of Pennsylvania for 1879-80, p. 67 and 1881-2, p. 111.

the Dipnoi merely by suture or contact, with other cartilage bones. Its character is therefore more nearly that of the Holocephali than of the Elasmobranchi or the Hyopomata.

In the light of the above considerations, to which sub-class must be referred the genus Didymodus? Does it possess a freely articulating hyomandibular bone, and maxillary, palatoquadrate and mandibular arches? The question must be primarily determined by these considerations, since the fins and their supports are unknown to us.

The lateral posterior processes of the skull are in its superior plane, and their extremities do not present an articular facet for the lower jaw. It is improbable that they were continued downwards as cartilage for the former articulation, as in the Holocephali and Dipnoi. Both from the presence of an articular condyle, and from the mechanical necessities of the case, I have little doubt but that there was a freely articulating hyomandibular bone. I have already described this element in fact as visible in a single specimen. The choice is thus limited to the Elasmobranchi and Hyopomata. It is decided in favor of the former by the absence of maxillary arch and of opercular apparatus. So then Didymodus is a shark, in spite of its peculiarities. Kner* speaks of the presence in the nearly allied Pleuracanthus (= Diplodus), of premaxillary and maxillary bones; but this is no doubt a misinterpretation of the homologies, as he says they *articulate with the lower jaw*. In my jaws there is but one bone on each side, a palatopterygoid.

In his researches on the structure of the skulls of sharks, Gegenbaur† shows the different methods of articulation of the palatopterygoid arch in the sub-class Elasmobranchi. In Heterodontus the palatopterygoid arch is attached to the skull throughout by its superior border, anterior to the orbit, but is free posterior to the orbit. In Hexanchus and Heptanchus it is free anteriorly, but articulates by its elevated posterior portion with the postorbital process. In the remainder of known recent Elasmobranchs it is free throughout, and merely in contact in front. These relations are also described by Huxley.‡ Professor Gill utilizes them as definitions of three (of four) primary divisions of the sub-class Elasmobranchi,§ which he names the Opistharthri, (fam. Hexanchidæ); Proarthri (Heterodontidæ); Anarthi (sharks proper); and Rhinæ (Squatinas). According to these definitions, Didymodus must be referred to the Opistharthri. The skull, however, presents other characters which must claim attention. Its

*Sitzungsberichte Wiener Akademie, LV, p. 540.

†Untersuchungen zur Anatomie der Wirbelthiere, Leipzic, 1872.

‡On the Anatomy of Ceratodus. Proceedings Zoöl. Society of London, 1876, p. 43–4, with figures.

§Bulletin of the U. S. National Museum, No. 16, 1883, p. 967. Gills fourth group, Rhinæ, does not appear to me to possess the value of the other three, nor are the "Raiæ" and "Pristes" more distinct. I therefore propose that the order Selachii, as defined in the following pages (of the sub-class Elasmobranchi), be divided into three sub-orders: Opistharthri, Proarthri and Anarthri, the latter to include the true sharks, the Squatinæ, the sawfishes and the rays.

reference to the Elasmobranchi is confirmed by the following characters: (1) The nares are not oral. (2) There is a large fontanelle on the summit of the muzzle. (3) There are processes corresponding to the lateral alæ of the basicranial axis.

In another character Didymodus differs from this and all other sub-classes of the Pisces. This is the penetration of the granular ossification throughout the chondrocranium.

In the following characters it agrees with the Dipnoi: (1) The distinct exoccipital, pariëtal, and frontal elements. (2) The occipital cotylus. (3) The posterior bifurcation of the frontal cartilage.

In the following characters Didymodus resembles the Hyopomatous or true fishes: (1) In the basioccipital bone with condyle. (2) In the ?os intercalare or pteroticum. (3) The presence of a distinct element articulating with the proximal end of the hyomandibular. (4) The presence of membrane bones in the position of frontals.

The characters above cited as constituting resemblances to the true fishes, will not, it appears to me, permit the reference of this genus to any of the divisions of sharks established by Prof. Gill. I therefore proposed a new order of the Elasmobranchi* for its reception, with the following name and definition.

A basioccipital bone and condyle. Occipital, ? pterotic, and frontal bones distinct. Supraorbital (or nasal) bones present............*Ichthyotomi.*

The remaining Elasmobranchi, in which the above characters are wanting, may be termed by way of contrast, utilizing an old name, *Selachii.*

Were it not for the probable presence of the free hyomandibular bone, the order Ichthyotomi might be regarded, in the absence of knowledge of its limbs, as the possible ancestor of the Rhachitomous Batrachia. But as the Batrachia have no distinct suspensorium, or are, to use Müller's convenient term, monimostylic, their origin must still be sought for in some yet undiscovered type of Dipnoi. It is on the other hand very probable that the Ichthyotomi are the group from which the Hyopomata derived their origin. The distinct basioccipital with its two foramina, the superior origin of the hyomandibular, and the superior nostrils, all point towards the true fishes. The tribe of Hyopomata which must be their most immediate descendents, are the Crossopterygia, as I define that division.

I must now compare the Ichthyotomi with such groups of the Hyopomata as they may be supposed to approach most closely. I begin by referring to the marine eels of the order Colocephali. In 1871† I characterized this order as follows: "Pariëtals largely in contact; opercular bones rudimental; the preoperculum generally wanting. Pterygoids rudimental or wanting; ethmoid very wide. Symplectic, maxillary, basal branchihyals, superior and inferior pharyngeal bones, all wanting, except the fourth pharyngeal. This is jaw-like, and is supported by a strong superior branchihyal; other superior branchihyals wanting or cartilaginous."

* American Naturalist, 1884, 413.

† Proceedings American Ass. Adv. Science, xx, pp. 328–331.

The statement "maxillary wanting," is in contradiction to the definition of the sub-class Hyopomata, which asserts the presence of those bones. Stannius* has asserted the absence of the "oberkiefer" in the eel; Günther† describes their presence. As the absence of the maxillary bone would constitute a point of resemblance, if not affinity to the Elasmobranchi, I have reëxamined my material to determine the homologies of the lateral dentigerous bone of the upper jaw of the eels. My specimens of species of the Colocephali include the following from the Hyrtl collection: *Myrus vulgaris; Sphagebranchus rostratus; Moringua rætaborua; Muræna sp.; Muræna unicolor; Muræna sp.; Poecilophis polyzonus*, and *Gymnomuræna tigrina*. The pterygoid bone exists in a rudimental condition in the *Gymnomuræna tigrina, Myrus vulgaris*, and one of the species of Muræna; and whether lost in the preparation of the other crania or not, cannot be stated. In the *Anguilla vulgaris* the pterygoid bone is considerably larger, and extends to a point halfway between its base and the extremity of the muzzle. In the *Conger vulgaris* it extends still further forwards, reaching a transverse process of the anterior part of the vomer. No palatine bone appears. The premaxillary bone is not distinguished from the ethmoid in the Colocephali, nor in the Enchelycephali (Anguillidæ, etc.). It is quite possible, therefore, that the external dentigerous bone or upper jaw, in both of these orders, may be the palatine, and the maxillary be wanting. The family of the Mormyridæ appears to furnish the solution. In this group the structure and connections of the pterygoid bone are much as in Conger, and there are in addition distinct premaxillary and maxillary bones. It is clear that in this family it is the palatine, and not the maxillary bone, that is wanting. Similar evidence is furnished by the family Monopteridæ. The definition of all four of the orders, Colocephali, Enchelycephali, Ichthyocephali and Scyphophori must, therefore, embrace this character. The Gymnarchidæ agrees with the Mormyridæ in this respect, and both families have the transverse process of the vomer which receives the pterygoid, as in the genus Conger.‡ The supposed resemblance to the sharks presented by the Colocephali is then not real, and the question as to the point of affinity of the Ichthyotomi to the true fishes remains open as before.

I now refer to the remarkable characters presented by the deep sea fishes of the family Eurypharyngidæ, as recently published by Messrs. Gill and Ryder.§ These authors find the characters of the skeleton so remarkable, that they think it necessary to establish a new order for its reception, which they call the Lyomeri. The definition which they give is the following: "Fishes with five branchial arches (none modified as branchiostegal or pharyngeal) far behind the skull; an imperfectly ossified skull articulating with the first vertebra by a basioccipital condyle alone; only

* Handbuch der Zootomie, Fische 1854, p. 76.

† Catalogue Fishes, British Museum, vol. viii, p. 19.

‡ These transverse processes are enormously developed in Gymnarchus.

§ Proceedings U. S. National Museum, Nov. 1883, p. 262.

two cephalic arches, both freely movable ; (1) an anterior dentigerous one—the palatine, and (2) the suspensorial, consisting of the hyomandibular and quadrate bones ; without maxillary bones or distinct posterior bony elements to the mandible ; with an imperfect scapular arch remote from the skull ; and with separately ossified but imperfect vertebræ."

M. Vaillant came to no conclusion as to the affinities of this group ; and Messrs. Gill and Ryder remark, "We are unable to appreciate any affinity of Gastrostomus to any Anacanthines, Physostomes, or typical Apods, nor does it seem to be at all related to Malacosteus, which has been universally considered to be a little modified Stomiatid." It is, however, clear to me that the relationships of this family Eurypharyngidæ are to the order Colocephali, and that they represent the extreme degree of the modification of structure which that order exhibits. In other words, the modification of the ordinary piscine type which is found in the Anguillidæ (order Enchelycephali), is carried to a higher degree in the Colocephali, and reaches its extreme in the Eurypharyngidæ. The points of identity between the two groups last-named are so many, that it becomes desirable to ascertain whether they are susceptible of ordinal separation from each other. The characters above given to the order Lyomeri are in fact identical with those which define the order Colocephali, with a few possible exceptions. First, however, I note that the supposed palatine arch, is probably the maxillary, as in the Colocephali, and that it is the palatopterygoid arch which is absent. The five branchial arches exist in the Colocephali, but the three anterior are rudimental, and the basal branchihyal bones of the fourth and fifth are closely united. There are, however, five arches. There is a ceratohyal arch in Muræna and Gymnomuræna, but of very slender proportions. Whether this element is absolutely wanting in Gastrostomus, or whether the first branchial arch is its homologue, remains to be ascertained. Should the last two be coherent as in the Colocephali, we would then have the same number of hyoid arches in both, viz., six. The "imperfectly ossified cranium" is shown in the detailed description given by Messrs. Gill and Ryder, to support the same bones which are found in the Murænoid skull. The degree of ossification of the skeleton does not constitute a basis for ordinal distinction, if the same elements be present. For this reason the perforation of the vertebral centra by the remnant of the chorda dorsalis does not seem to be of ordinal importance.

In the more detailed description, there are a few charecters worthy of notice. First, "The notochord is persistent in the skull for half the length of the basioccipital." This indicates further the primitive condition of the vertebral column, but scarcely gives basis for an ordinal definition. Second (p. 266.), "The neurapophyses are slender, diverging (instead of convergent), cartilaginous distally, and embracing the neural sheaths on the sides, while by the neurapophyses is supported a membranous sheath which roofs over the nervous cord," etc. The nerual canal is well closed above in the Murænidæ, but in the Anguillidæ it is largely open above. The neurapophyses it is true unite, but at a distance above the neural cord, and as attenuated rods. Third, "There is no vomer developed, but a triangular cartilaginous element pendent from the cranial rostrum affords attachment for the palatine (read maxillary) element anteriorly," etc. This element probably exists in the Colocephali and similarly takes the place of the vomer, only differing in being ossified. I have been accustomed to regard it as the homologue of the bone called ethmoid in fishes.

The character which distinguishes the Colocephali from the Enchelycephali, now that their maxillary and palatine structure are shown to be essentially the same, is found in the hyoid apparatus. In the Enchelycephali, the structure is as in ordinary fishes; there is a glossohyal, and there are basihyals, and axial branchihyals, and superior pharyngeals. In the Colocephali all these elements are wanting, excepting the fourth superior pharyngeal, which has the form of an antero-posteriorly placed dentigerous jaw, which opposes the lateral branchihyal of the fifth arch or, as it is generally called, the inferior pharyngeal. It is evident that the Eurypharyngidæ are more similar to the Colocephali than to any other order in this respect also, but the description of these parts is not yet sufficiently detailed to enable me to determine what difference there may be in this respect, if any. The mobility of the quadrate bone on the hyomandibular cannot be regarded as of great systematic significance, although it is doubtless important in the economy of the fish.

It is then evident that the Eurypharyngidæ belong very near to, if not within, the order Colocephali. Towards the end of their description, Messrs. Gill and Ryder (p. 270), recognize this relationship, but deny that it indicates that this family is "from the same primitive stock as the Muraenids." I incline to the belief that it is the ultimate result of the line of development of which the Anguillidæ form one of the first terms, and the Murænidæ a later and more specialized one.

It is therefore clear that the point of relationship of the Ichthyotomi to the true fishes is not to be found in the Eurypharyngidæ or the Colocephali.

In the following point Didymodus resembles Polypterus. The fossa above described as on each side of the basioccipital, is found in Polypterus. There it serves as a place of insertion of a strong ligament on each side, which is attached externally to the epiclavicle, and serves to hold the scapular arch in its place. A similar structure exists in the Siluirdæ, where the ligaments are ossified. It suggests for Didymodus a scapular arch suspended more anteriorly than in sharks, possibly even to the skull.

The genealogy of the fishes will then be as follows, first, however, it is to be understood that in asserting the derivations of one group from another, I mean that in accordance with the rule which I have termed "the doctrine of the unspecialized," the later type in each case is the descendant of the primitive and not the later sub-form of its predecessor. In this way is to be explained the apparent anomaly of regarding the notochordal sturgeons as descendants of Crossopterygia, whose modern representatives are osseous. The primitive Crossopterygia, and probably even the Actinopteri, were doubtless as cartilaginous as are the existing sturgeons:

Hyopomata = { Actinopteri. Chondrostei. Crossopterygia.

Elasmobranchi = { Ichthyotomi. Selachii.

Holocephali. / Dipnoi. / Batrachia.

In this phylogeny, the Holocephali, which have not differentiated a suspensorium, are regarded as the primitive fishes, although the living representatives display some specialized characters, as, for instance, a membranous gill-cover which conceals the primitive slits. The line to the right continues the monimostylic character and passes into the reptiles, whose primitive types are also monimostylic, as Johannes Müller called them. In the later forms or streptostylicate reptiles of Müller (Lacertilia, Ophidia), the quadrate becomes freely articulated.*

In the left hand series, the Elasmobranchs immediately present us with the free suspensorium or hyomandibular, which is a well-known character of the remainder of the line, the modifications being the addition of separate elements, as the metapterygoid, "quadrate," and symplectic.

The penetration of ossification into the chondrocranium of Didymodus, in regions not ossified in either fishes or batrachia (sphenoid and presphenoid), and into regions not ossified in any vertebrate (fróntal and pariëtal cartilages), may be, so to speak, only a local phenomenon, and not indicative of extensive phylogenetic consequences. For if it be so regarded, it evidently proves too much, giving affinities in the base of the skull to the reptiles, and in the roof exhibiting a character more highly developed than any known form of vertebrata.

The Ichthyotomi include, so far as yet known, but one family, the Hybodontidæ of Agassiz. According to that author this family includes four genera, Hybodus, Pleuracanthus, Cladodus and Sphenonchus. It ranges from the coal-measures to the Jura inclusive.

The genus Didymodus may be described as follows:

Frontal plane well defined on each side by the temporal fossæ, and terminating in two cornua posteriorly. Anterior nares on the superior surface of the muzzle. Supraorbital (or nasal) bones well separated on the median line and constituting the only membrane ossification. Teeth with large lateral denticles.

The species *Didymodus compressus* Newberry, may be defined as follows:

Skull with massive walls. Form elongate, depressed, the orbit not ex-

* The phylogeny of the Reptilian series can be found in the Proceedings American Association Advancement of Science, xix, 1871, p. 233. The Batrachia are supposed to be their ancestors.

tending behind the anterior third of the length. Basicranial and basifacial axes in one line, flattened, the supraorbital border flat, concave on the edge; postorbital processes obtuse, the temporal ridges commencing with thin posterior border, which they excavate. The ridges then turn, extend parallel posteriorly, terminating in the horn-like processes already described, with a slight divergence. The apices mark the posterior third of the length of the skull. The occipital condyle is wider than deep, and its superior border retreats forwards so as to cause its cup to look upwards. The exoccipital diameter at the foramen magnum is less than that of the basicranial axis, the osseous element of which, probably sphenoid, is recurved on the sides to their middle. The sides of the latter expand a little to meet their lateral alæ. Immediately above their contact is situated the supposed condyle for the hyomandibular element. The basicranial axis is convex opposite the postorbital processes, from the bases of which a concavity separates it. It has a slight median groove at this point. It is much narrower than the interorbital width above. A short distance in front of the postorbital processes it begins to contract, and gradually reaches an acuminate apex. Superior to this apex, commencing posterior to it, the space between it and the supraorbital or nasal elements is occupied by a massive element (? ethmoid) which forms the floor of the nasal median fontanelle.

The surfaces are smooth, but readily weather so as to be granular. The granules are subround, with flattened surface.

Measurements of skull.	M.
Total length of skull to end of frontal bone (No. 1)....	.180
" " " muzzle to orbit; axial................	.024
" " " skull to postorbital process............	.058
" " " " to apices of frontal cartilage......	.117
" " " " to ? pterotic apex (axial).........	.155
Width of skull at prefontals.........................	.045
" " " " supraorbital borders................	.055
" " " " ? pterotic apices....................	088
" " occipital condyle...........................	.034
Depth " " "	.025

Measurements of jaws.	
Length of mandibular ramus from cotylus, inclusive.	.145
Depth " mandibular ramus at cotylus...............	.028
" " " " " middle..............	.035
Length " palatopterygoid bone from cotylus, inclusive.	.145
Depth " " " at postorbital articulation......	.071
Depth of palatopterygoid bone at orbit................	.035
Length " " " posterior to orbit	.070

A second species has been brought to light by the researches of Mr. W.

F. Cummins in the Permian beds of Texas. Parts of the jaws with two of its teeth are preserved. The lower jaw is distinguished from that of the *D. compressus* by its small transverse as compared with its other diameters. The ramus is quite compressed, and is not thicker at the inferior edge than the superior, and is slightly concave on the inner side. Its external face is nearly vertical. The angle is rounded forwards, and there is no angle behind the cotylus, which is raised above the superior line of the ramus. The cotylus is rather large, and has a shallow anterior superior, and a posterior subposterior facet. There is no indication of a coronoid process. The inferior edge of the ramus is swollen on the outer side, below the anterior border of the condyle, so as to mark with the thickened posterior edge of the ramus a fossa in the position of the masseteric.

The teeth are pecular in the form of the root (Figs. 8–9). This part has no anterior projection, and the posterior portion is a flat, thin-edged plate, wider than long. It carries a button, but no notch. There is a minute median denticle. The form of the root is thus very different from that of the tooth of the *D. compressus* (figs. 5, 7).

Measurements.		M.
Depth of ramus at cotylus (vertical)		.062
" " " 120 mm. anterior to cotylus		.048
Transverse diameter at the same point		.009
Long diameter (oblique) of cotylus		.031
Diameters of base of tooth	anteroposterior	.011
	transverse	. 37
Diameters of crown of lateral denticle	anteroposterior	.0048
	transverse	.006

I call this species *Didymodus platypternus*. Should the name Didymodus be found hereafter to apply to species of Pleuracanthus, the latter generic name must be used for this species.

III. Historical.

In 1837 Prof. Agassiz (Poiss. foss., iii, 66), described a spine which he believed to have belonged to a fish like the sting-rays, as *Pleuracanthus lævissimus*. The only example was obtained from the Dudley Coal field.

In 1845 Prof. Agassiz (Poiss. foss., iii, 204), made known certain teeth, which he referred to sharks of the family of Hybodonts. Two species were distinguished, *D. gibbossus* and *D. minutus*. Both were obtained from the English Coal measures.

In 1848 Prof. Beyrich (Berichte vernandl. k. Preuss. Akad. wiss., 1848), proposed the generic name Xenacanthus for a German Carboniferous form, referred to Orthacanthus by Goldfuss (1847), but which approached nearer to Pleuracanthus.

In 1849 Dr. Jordan (Jahrbuch für Min. u. Geol., p. 843), described, under the name *Triodus sessilis*, a form subsequently ascertained to be identical with the Xenacanthus.

In 1857 Sir Philip de Malpas Gray Egerton (Ann. and Mag. Nat. Hist., xx, 423), contended that the spines of Pleuracanthus belonged to the same fish as the Diplodus teeth, and that Xenacanthus was likewise referable to the same type.

In 1867 Prof. Kner (Sitzb. k. Akad. wiss. Wien, lv, 540–584), published a memoir, illustrated by ten plates, in which he proved that Diplodus and Xenacanthus were generically identical.

In 1875 Messrs. St. John and Worthen proposed the genus Thrinacodus for the *Diplodus incurvus* and *D. duplicatus* of Newberry and Worthen and the *T. nanus* St. J. and W., from Illinois.

In 1883, in the Proceedings of the Philadelphia Academy (p. 108), I proposed the name Didymodus for the *Diplodus compressus* Newberry.

In Science for 1884, p. 274 (March 7th), I called attention to the close resemblance of the teeth of this genus to those of the recent shark, called by Garman Chlamydoselachus, and expressed my belief in the identity of the two genera.

In the American Naturalist for April, 1884, p. 413, I gave a brief abstract of the characters of the skull of Didymodus, and proposed to regard it as the type of a new order to be called the Ichthyotomi.

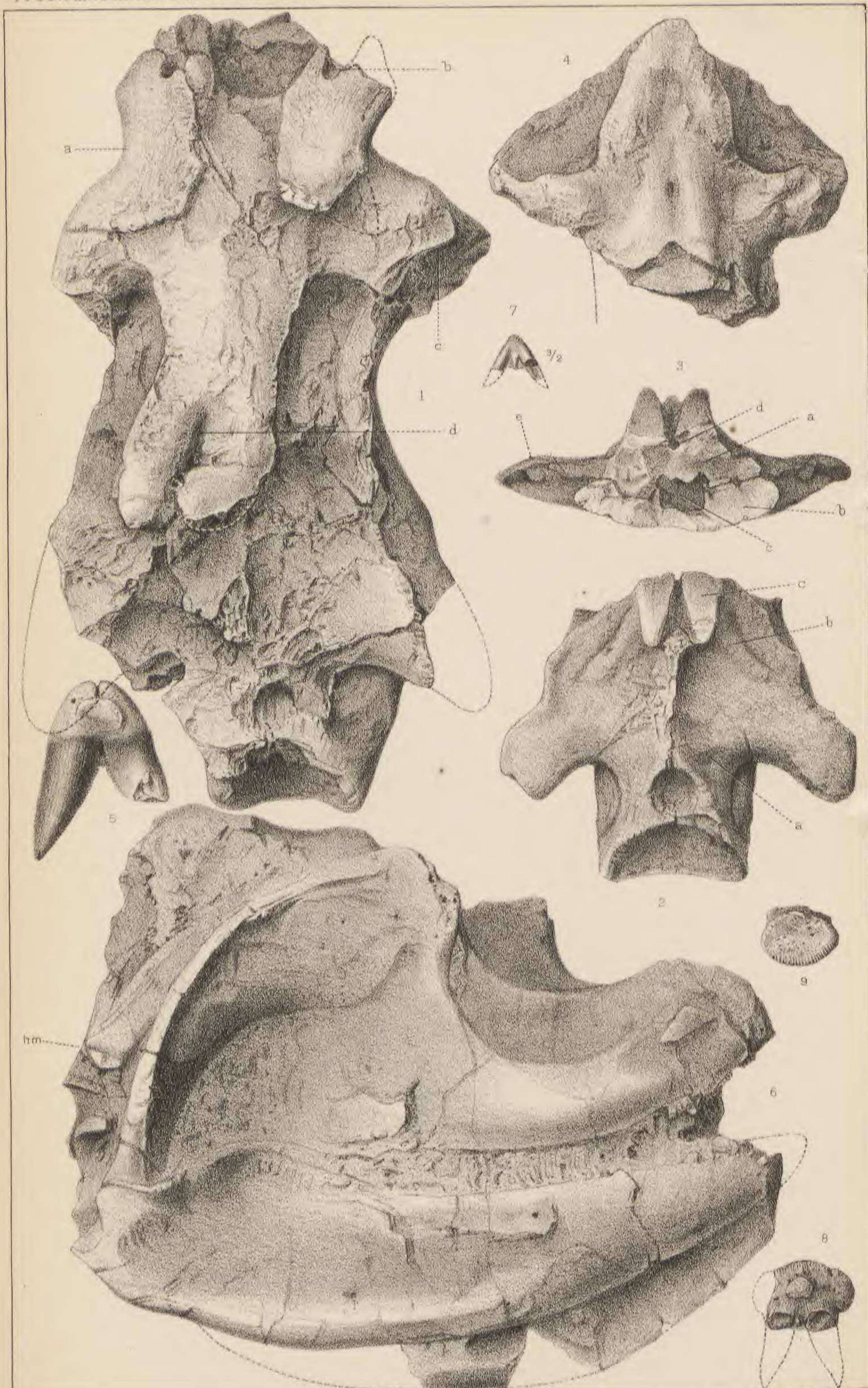
In Science, 1884, p. 429 (April 11), Prof. Gill objects to the identification of the genera Didymodus and Chlamydoselachus; on the ground of the different forms of the teeth. He states that he doubts the pertinence of the two genera to the same order. He points out that the oldest name for Diplodus Ag. is Pleuracanthus Ag., and that the order Ichthyotomi had been already defined and named by Lütken, with the name Xenacanthini.

On these various propositions the following remarks may be made.

(1.) There is no generic difference to be detected, in my opinion, between the teeth which are typical of Diplodus Agass. and Thrinacodus St. J. and W. and the recent Chlamydoselachus. Differences there are, but apparently not of generic value. The identification of the recent and extinct genera rests, as far as this point goes, on the same basis as that of the recent and extinct Ceratodus.

(2.) At the time of my proposal of the name Didymodus, I was not convinced that fishes of this type bore the spines referred to the genus Pleuracanthus Ag. None of the authors cited figure any specimens which present both tricuspidate teeth and a nuchal spine. None of my ten specimens possess a spine. However, Kner describes two specimens as exhibiting both tricuspidate teeth and a spine, and Sir P. Egerton's statements (*l. c.*), on this point are positive. So we must regard Pleuracanthus as the name of this genus, with Diplodus as a synonym.

(3.) Diplodus being regarded as a synomym of Pleuracanthus, it follows that Chlamydoselachus Garm. is distinct, on account of the *different structure of the dorsal fin*, which is single and elongate in Pleuracanthus, according to Geinitz and Kner. The presence of the nuchal spine in Pleuracanthus is also probably a character of distinction, although we do not yet know whether such a spine is concealed in Chlamydoselachus or not.



T. Sinclair & Son, Lith. Phila.

SKULL OF DIDYMODUS.